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ABUNDANCE ESTIMATION FOR HARBOR PORPOISE *(Phocoena phocoena)* BASED ON SHIP SURVEYS ALONG THE COASTS OF CALIFORNIA, OREGON AND WASHINGTON

By

Jay Barlow

ADMINISTRATIVE REPORT LJ-87-05

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ABUNDANCE ESTIMATION FOR HARBOR PORPOISE (*PHOCOENA PHOCOENA*) BASED ON SHIP SURVEYS ALONG THE COASTS OF CALIFORNIA, OREGON AND WASHINGTON

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ABSTRACT

The density and total population size of harbor porpoise along the coasts of California, Oregon, and Washington are estimated from four ship surveys using line transect methods. Estimates are based on sighting surveys completed between September 1984 and May 1986 using 52-54m research ships and teams consisting typically of 5 observers. Data include 852 porpoise groups sighted during 6,590km of transects. Sighting rates varied more due to effects of sea state than due to the presence of rain, fog, or sun glare. Experiments using additional observers indicate that 23% of trackline groups may be missed by a team of 5 observers. Porpoise density is calculated from transects along the 18m isobath and is extrapolated to other depth zones based on a model of porpoise abundance as a function of depth. Total population size is estimated as 49,862 (s.e. = 8,891) animals. Because several assumptions of line-transect sampling are violated, this may be an underestimate of the true population size.

INTRODUCTION

Approximately 200-300 harbor porpoise are taken annually in central California set-net fisheries (Hanan and Diamond, in prep.). Little is known about porpoise abundance in this area. Dohl, Guess, Duman and Helm (1983) estimated that 1600-3000 porpoise reside in central and northern California based on their aerial surveys of coastal cetaceans. However, because harbor porpoise are frequently missed in aerial surveys (Kraus, Gilbert and Prescott 1983), this estimate is probably low. Insufficient information is also available regarding porpoise stock structure in this area. Gaskin (1984) proposed working subdivisions of Pacific harbor porpoise populations based primarily on habitat discontinuities. His southeastern subdivision included the coast between Cape Flattery, Washington and Los Angeles, California. No attempts have been made to examine discontinuities in distribution or other evidence of stock structure within this subdivision. More information is needed on abundance and

distribution to determine the significance of porpoise mortality in set-nets.

Beginning in 1984, the National Marine Fisheries Service (NMFS) has conducted ship and aerial surveys of harbor porpoise abundance in California, Oregon, and Washington. This report presents results from four ship surveys (Table 1). Results of the aerial surveys are presented in a separate paper[1].

Porpoise density is estimated from survey data using line transect models (Burnham, Anderson, and Laake 1980). Total abundance is estimated by extrapolating from density observed along transect lines to the entire area inhabited. Abundance in offshore regions is based on a model of porpoise density as a function of water depth. In addition to abundance estimation, survey data are used to examine the effect of environmental conditions on sighting efficiency and the possibility of temporal changes in harbor porpoise distribution.

METHODS

Ship Survey Methods

Surveys were conducted from two National Oceanic and Atmospheric Administration (NOAA) research vessels, the 52m R/V David Starr Jordan (Surveys 1, 3 and 4) and the 54m R/V McArthur (Survey 2)[2]. Both vessels are of similar design with viewing stations located on top of the pilot house (viewing height was approximately 10m above sea surface). Transect lines followed as close as possible to the 18m isobath (roughly 2-4 km from the coast), although the actual depth along the transect varied from approximately 15 to 45m depending on the presence of local navigational hazards. The areas surveyed are shown in Figure 1. Survey design varied among the four trips:

> Surveys 1 and 3 were both in September and were designed to survey porpoise density and abundance from Point Conception to Cape Flattery. An attempt was made to survey the entire coastline on each of these cruises, but several sections of the coast were missed (Fig. 1) due to fog and heavy weather. Five observation positions were used on these two surveys.

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[1] Barlow, J., C. Oliver, T. D. Jackson, and B. L. Taylor. Population density estimates for harbor porpoise (Phocoena phocoena) based on aerial surveys of California, Oregon and Washington Coasts. Unpublished manuscript.

[2] Cruise reports available from Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

Survey 2 was in January/February and was primarily designed to look at seasonal changes in porpoise distribution. Only 3 observation positions were used from Cape Flattery to Point Reyes and from Point Sur to Point Conception. Data from this cruise were not used for density or abundance estimation.

Survey 4 was designed to investigate factors which affect porpoise density estimation. The vessel's activities were coordinated with a helicopter to gather information on the avoidance of the ship by harbor porpoise. Experiments were also conducted on Survey 4 to determine whether an additional team of 3 observers working independently would sight any porpoise that were missed by the primary team of 5 observers. Data from this survey were not used for density or abundance estimation.

Typically, eight to ten observers were used on each survey, with a rested observer starting every half hour and rotating through five primary observation positions at half hour intervals. The five positions consisted of port and starboard inboard observers, port and starboard outboard observers, and a recorder positioned amidship. The inboard observers searched with 7 power (7x) binoculars from straight ahead to 90° (Survey 1) or to 45° (Surveys 2, 3 and 4) on their respective sides of the vessel. On Survey 1 the outboard observers searched with 25x, pedestal-mounted binoculars. Although sightings could be made at great distances from the vessel using the 25x binoculars, these distant sightings contributed little to the estimation of track-line density, and use of 25x binoculars was discontinued. On subsequent surveys, both the inboard and outboard observers used 7x binoculars. The outboard observers searched from dead ahead to 90° on their respective sides of the vessel. The recorder searched in the immediate vicinity of the ship using unaided eyes and (intermittently) 7x binoculars. On Survey 2, when effort was reduced to 3 observers, the inside observation positions were eliminated. On Survey 4 a second team of 3 observers was added to monitor the effectiveness of the principal team. This monitor team searched using unaided eyes and (intermittently) 7x binoculars from the pilot-house deck (viewing height approximately 7m from sea surface). The principal team and the monitor team did not communicate sighting information, and independent records were kept.

Data were logged by the recorder on data coding forms. Data on search effort included the beginning and ending times and positions for continuous legs of effort, the ship's heading and speed, personal identification codes for the observers, sea surface temperature, water depth, Beaufort sea state, sun position relative to the ship, and codes indicating the presence

of rain or fog within 5 km. The ship's position was determined from a Loran navigational system or by triangulation using coastal landmarks and dead reckoning. Ship's speed was recorded directly from the Omega/Loran system or was calculated based on time and distance traveled between successive position fixes along straight transect lines. Sea surface temperature was measured using a flow-through thermosalinograph or a calibrated bucket thermometer. Water depth was measured using a 38 kHz acoustic depth sounder.

Data for sightings consisted of the above elements, plus estimated group size, distance to shore, an estimate of the angle between the trackline of the ship and the group, and an estimate of the distance from the ship to the group. Group size refers to all the individuals associated with a sighting event, regardless of whether those individuals constituted a social unit. In most cases, groups were closely associated individuals that surfaced together (mean = 2.92, median = 2.0). In two cases (Point Arena and Monterey Bay, California), groups consisted of 50-80 loosely associated individuals that were organized in sub-groups of 4-10). Group size was estimated and recorded independently by each observer; the average of these estimates was used in subsequent analyses. The angle from the trackline to the porpoise was estimated visually with the aid of a protractor mounted in front of the observer stations, or, when 25x binoculars were used, from a calibrated collar on the pedestal mount. On Surveys 1 and 2, distances to harbor porpoise were estimated visually using the radar distance-to-shore as a reference, or, when 25x binoculars were used, distances were estimated using calibrated reticles in the oculars. On Surveys 3 and 4, distances were estimated using calibrated reticles in the oculars of 7x binoculars. Data were also collected on the porpoises' direction of travel relative to the ship.

The length of a transect was estimated as the product of ship's speed and elapsed time. To stratify density estimates by sea state, rain, and fog, the effort record was divided into segments during which the sea state, rain, and fog codes did not change.

In six limited areas, information was collected on variation in porpoise density with water depth. During Survey 2, the region between Point Reyes and Point Sur, CA was surveyed intensively, with transect lines following both the 18 and 92m isobaths. During Survey 3, three sections of the coast were surveyed intensively (Fort Bragg to Cape Lookout, CA; Cape Blanco to Coquille Point, OR; and Cape Lookout to Tillamook Head, OR), with transect lines following the 18, 56, 92, and 185m isobaths. On Survey 4, the 18 and 46m isobaths were surveyed in Monterey Bay, CA and in the vicinity of the Russian River, CA. These data were used to parameterize a model (below) to extrapolate porpoise

density from the usual transect lines (along the 18m isobath) to deeper waters.

Helicopter Observations

During Survey 4, a Hughes 500-D helicopter was used to collect information on porpoise behavior in response to the survey ship. The helicopter flew approximately 10km ahead of the vessel, and three observers in the helicopter looked for porpoise. Once a group of porpoise was sighted, the helicopter hovered at 200-300m while observers made behavioral observations and periodically recorded the helicopter's position using an on-board Loran system. Fluorescein dye packages were dropped in the water to allow the helicopter to maintain its position when porpoise were diving. Radio communication was maintained with personnel on the ship who also kept records of the helicopter position using radar distances and bearings based on returns from an X-band radar transponder in the helicopter. The ship changed course, when necessary, to ensure that it passed in close proximity to the porpoise that were being observed. Porpoise observers on the ship were not aware of the helicopter's activities and were not told of sightings made by the helicopter observers (although they were able to see dye patches in some cases). Behavioral observations from the helicopter included time spent at the surface, time spent diving, and direction of porpoise movement

Density Estimation

Line transect methods were used to estimate the density of harbor porpoise from sightings. The assumptions of these methods are considered in detail in the discussion. The usual formula for estimating density (D) based on line transect surveys of grouped animals is given by

$$D = f(0) \cdot n \cdot G / 2 \cdot L \qquad (1),$$

where $f(0)$ = the probability density function for sightings evaluated at zero perpendicular distance,

n = number of sightings of groups,

G = average group size calculated as the total number of individuals in all groups divided by the number of groups ($\Sigma N/n$), and

L = length of the transect.

I did not use mean group size explicitly in abundance estimation, and density of harbor porpoise individuals, D, was estimated as

$$D = f(0) \cdot (R / 2) \qquad (2),$$

where R = the number of individuals seen per length of transect ($\Sigma N/L$).

Although this model appears to depart from that used previously in estimating density of small cetaceans based on ship surveys (Holt and Powers 1982; Hammond and Laake 1983; Holt, in press), it is, in fact, equivalent. Mean densities would be the same by either model, but estimating variance using Equation 1 is unnecessarily complex. Typically when using Equation 1, variances (and possibly covariances) must be estimated for f(0), G, and n, and the variance in D is then estimated using the product variance formula (Goodman 1960). Using Equation 2, variances are needed only for f(0) and R, and covariance between mean group size and number of groups is handled implicitly.

The parameter f(0) is, in effect, a measure of sighting efficiency and should not vary with porpoise abundance. Sighting efficiency is, however, likely to change with sighting conditions, such as Beaufort sea state. Given these expectations and because relatively large sample sizes are needed to estimate f(0) accurately, values for f(0) were estimated for each survey by pooling all sightings within defined sea state catagories. In order to estimate density on a finer scale, estimates of R were stratified by geographic region and multiplied by the pooled estimate of f(0).

The sighting probability density function evaluated at zero distance, f(0), was determined empirically by fitting sightability curves to the frequency distribution of sightings as a function of perpendicular distance from the trackline (Burnham and Anderson 1976). Differences in distributions of perpendicular distance were tested using the Kolmogorov-Smirnov 2-sample test. To account for rounding error in estimating perpendicular distance, angle and radial distance data were "smeared" (Butterworth 1982, Hammond and Laake 1983). Estimated sighting angles were typically rounded to the nearest 5 or 10° (Fig. 2); therefore, angles were smeared by adding a uniformly distributed random number between -5° to +5° to angle estimates. The degree of rounding in estimates of radial distance tended to increase with distance (Fig. 3 and Fig. 4), hence the degree of smearing was made proportional to estimated distance. A uniformly distributed random number between -0.2 and +0.2 times the estimated value was added to each radial distance.

Several models were investigated for estimating f(0) from sighting distributions. The FORTRAN program Transect (Laake, Burnham and Anderson 1979) was used to fit 2-, 3-, 4-, and 5-parameter Fourier series and 2-parameter exponential power series models. The FORTRAN programs Hazard and Hermite (S. Buckland,

pers. comm.) were used to fit the 2-parameter hazard rate model (constrained such that parameter p > 2, Buckland 1985) and the 1-, 2-, 3-, and 4-parameter Hermite polynomial model (Buckland 1985). Distributions of perpendicular sighting distance showed very high values near the origin, and neither the Fourier series nor the Hermite polynomial models were able to adequately fit this spike. The exponential power series is able to fit spiked data, however this model has been faulted on the basis of its high variance and its dependence on the criteria used to group data (Buckland 1985). The 2-parameter hazard rate model was therefore chosen for porpoise density estimation based on its ability to fit the observed distributions and its lack of dependence on grouping criteria.

Perpendicular distances were grouped into strata, the size of which increased with perpendicular distance: 0-25m, 25-50m, 50-100m, 100-200m, 200-400m, 400-800m, 800-1600m, and 1600-3200m. Several alternative groupings were investigated, and the choice of cutpoints made very little difference in estimates of f(0). The above strata (increasing with distance) gave lower variances in f(0) than when each stratum was of equal size (possibly because the hazard rate model assumes a distinct shoulder in the sighting distribution, and that shoulder is lost if the first distance strata are large).

No established criteria exist for choosing an appropriate perpendicular distance at which to truncate sighting distributions. Burnham et al. (1980) recommends that no more than 1-3% of sightings be eliminated by truncation. Using this recommendation, models were not able to adequately fit the observed sighting distributions. In this report, truncation distance was chosen in four ad hoc steps. 1) The hazard rate model was fit to perpendicular distance data truncated at distances of 400, 800, 1600, and 3200m. 2) Truncation distances were identified which gave acceptable X^2 values ($p > 0.1$). 3) Of the acceptable truncation distances, the standard error in f(0) was estimated empirically by randomly drawing 10 samples (of the same size as the original sample) from the observed distribution of perpendicular distances and by calculating the standard deviation of f(0) estimated from each random sample. 4) Truncation distances were chosen as those which gave the lowest coefficient of variation in f(0).

Variance in R, the number of porpoise seen per kilometer, was estimated using jackknife statistics (Efron 1982). Jackknife estimates were calculated by first estimating the value of R using all data. The value, R_k, was again estimated excluding the k-th segment of search effort. This process was repeated for each effort segment. To ensure that each k-th segment was of equivalent length, effort segments with the same sea state, rain, and fog codes were combined in a linear array and were then

divided into ten segments of approximately equal length. The variance in the estimate was calculated as

$$s^2 = \frac{9}{10} \sum_{k=1}^{10} (R_k - \bar{R})^2 \qquad (3).$$

The variance of D was estimated using the Goodman (1960) product variance formula (assuming no covariance) using this jackknife variance for R and the above Monte Carlo variance for f(0).

Fraction of Missed Animals

On Survey 4, a second, independent team of 3 observers were used to estimate the fraction of porpoise that are missed by the primary team of 5 observers. The fraction of missed animals in a sighting survey is analogous to the fraction of unmarked animals in a mark/re-capture experiment. This fraction was estimated using the Lincoln (or Peterson) index method (Adams 1951). All the porpoise seen by the second team of 3 observers were treated as the second sample in a mark/recapture study. The number of animals (within this sample) which were also seen by the primary team were treated as marked individuals. The fraction of animals seen by the primary team was estimated as the ratio of "marked" individuals to the size of the second sample. Confidence limits were estimated using Adams' (1951) method, which assumes a binomial sampling distribution. Standard error was estimated using standard binomial formulas.

Abundance Estimation

A model was used to estimate the number of porpoise along the entire coastline based on the density that was observed along the 18m isobath. In shallow areas, such as the Bering Sea and Georges Bank, harbor porpoise are found a considerable distance from land (Gaskin 1984), hence offshore distribution is better modelled as a function of depth than as a function of distance from shore. (Although harbor porpoise are also found in very deep water in fjords and inland waterways of Alaska (Taylor and Dawson 1984), this represents a special case that is not applicable to coastal waters considered here.) The model used to estimate abundance was based on data collected on Surveys 2, 3, and 4 and on data from a similar survey by La Barr and Ainley[3] in central California. The number of porpoise seen per kilometer of

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[3] LaBarr, M. S. and D. G. Ainley. 1985. Depth distribution of harbor porpoise off central California: A report of cruises in April and May-June 1985. Report to U.S. National Marine Fisheries Service, Northwest and Alaska Fishery Center, 7600 Sand Point Way, N.E., Seattle, Washington. Contract No. 41-USC252.

transect was taken as an index of relative density along each isobath. A simple descriptive model was then constructed to give relative density as a function of water depth.

Three depth strata were used in abundance estimation (0-50, 50-100, and 100-300m). The choice of these strata was dictated by the availability of digitized data for bathymetric contours. The surface area within the strata was calculated from these digitized data. Kelp beds were assumed to be unsuitable as harbor porpoise habitat; hence, kelp bed area was subtracted from the total area within the 0-50m stratum. Kelp bed areas for the entire west coast were taken from Crandall (1915). More recent estimates for limited areas in central California are in good agreement with these previous values (Glenn Van Blaricom, pers. comm.).

For each of 3 depth strata, the abundance of harbor porpoise was estimated as the product of their density along the survey line (the 18m isobath), the density in that depth strata relative to that along the survey line, the surface area included within that depth strata, and the inverse of the estimated fraction of trackline animals that were missed. Since survey effort and harbor porpoise density both varied geographically, abundance estimates were made for each of 8 geographic regions (Fig. 5). Areas within the depth strata and kelp bed areas are given in Table 2 for each of these regions. The estimate of total abundance along the coast, N_T, is therefore given by:

$$N_T = \frac{1}{F} \cdot \sum_{j=1}^{8} D_j \sum_{k=1}^{3} (I_k \cdot A_{j,k}) \qquad (4),$$

where
- D_j = density of individuals observed on the transect line in the j-th geographic strata,
- I_k = ratio of density in depth strata k to that on transect line,
- $A_{j,k}$ = area in geographic region j and depth strata k, and
- F = the estimated fraction of trackline animals missed by the usual team of 5 observers.

Equation 4 was applied independently to the different surveys and, within surveys, to different sea state strata. When combining estimates from different sea states or different cruises, abundance was calculated as the average of the densities in each of the geographic stratum, weighted by the length of the transect line within that strata.

In estimating standard error for total abundance, variances of products were calculated using the Goodman (1960) product variance formula, and variances of ratios were estimated using a Taylor approximation (Yates 1953, p. 198). Area was assumed to be known without error. Statistical error in the indices of abundance for the three depth strata could not be estimated given the paucity of current information. To account for uncertainty in the model of depth distribution, three versions of the model are proposed to span a range of possibilities.

RESULTS

On the four surveys, 852 groups of harbor porpoise were sighted (approximately 1,800 individuals). A distance of 6,590km was surveyed during 56 days. The number of sightings per kilometer surveyed varied geographically and these geographic patterns appeared to change appreciably between cruises (Fig. 1).

Sighting Distributions

The number of sightings on the inshore and offshore sides of the vessels were approximately equivalent (383 and 392 respectively). The cumulative distributions of perpendicular sighting distances were not significantly different for these two sides ($p = 0.06$). Therefore, sighting distributions were assumed to be symmetrically distributed about the track-line, and the distributions of perpendicular sighting distances from both sides of the vessel were pooled for subsequent analyses.

The distributions of perpendicular sighting distances for the first three surveys (Fig. 6) were significantly different from one another ($p < 0.01$ for all). This was probably the result of the modifications in survey methods between these cruises. Surveys 3 and 4 used the same methods, and sighting distributions (Fig. 6) were not significantly different ($p = 0.39$). Given that changes in methods result in differences in sighting distributions, all surveys were treated separately in subsequent analyses.

Environmental Conditions Affecting Sightings

Sighting efficiency was not significantly affected by rain, fog, or sun glare. Rain/fog conditions were considered "poor" if rain or fog were present within 5km of the vessel and "good" if neither were present. The distributions of perpendicular sighting distances were not significantly different between these two strata ($p = 0.32$, 0.44, 0.78, and 0.64 respectively for Surveys 1, 2, 3, and 4), and the number of porpoise per kilometer surveyed was higher in the "poor" category for two of the

surveys. Sun glare from the water's surface was considered to contribute to "poor" sighting conditions if the sun was within 45° of the trackline in front of the ship. Conditions were considered "good" when the sun was in other positions or was obscured by clouds. The distributions of perpendicular sighting distances were not significantly different between these "good" and "poor" sun glare categories ($p = 0.87$, 0.47, 0.30, and 0.55 respectively for Surveys 1, 2, 3, and 4). The number of porpoise per kilometer surveyed were slightly higher in the poor category for three of the surveys. In paired comparisons when glare was present on only one side of the bow, approximately equal numbers of sightings were made on the sides with and without glare (60 vs. 59, respectively). All categories of rain, fog, and glare are included in subsequent analyses.

Sea state did have a significant effect on porpoise sightings. Sea state was categorized as calm (without white-caps, Beaufort sea states 0, 1 and 2) or rough (with white-caps, Beaufort sea states 3, 4 and 5) following the classification used by Holt[4]. Distributions of perpendicular distances were not significantly different between these categories for any of the surveys ($p > 0.05$); however for all surveys combined, the number of porpoise detected per kilometer was much lower during rough seas (0.32 km^{-1}) than during calm seas (1.22 km^{-1}). There were insufficient sightings to estimate density for rough seas separately; therefore, rough sea data were excluded in subsequent analyses. For all three surveys, the numbers of porpoise detected per kilometer was higher at Beaufort states 0 and 1 than at Beaufort 2, and for Survey 3, the distributions of perpendicular sighting distance were significantly different between these categories ($p = 0.03$). Porpoise density is, therefore, estimated separately for Beaufort states 0 and 1 and for Beaufort 2 conditions. (For comparison, porpoise abundance was also estimated pooling Beaufort sea states 0, 1, and 2. Estimated abundance was approximately the same by both methods, but the variance was slightly lower using the stratified sea state categories. For this reason, only the stratified estimates are presented here.)

Helicopter Observations

Helicopter observation of the behavior of harbor porpoise in response to the survey ship were limited to 6 groups of animals. Plots of vessel tracks and movements of the groups are given in the cruise report[2]. Only in one case was a distinct behavioral

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[4] Holt, R. S. 1984. Testing the validity of line transect theory to estimate density of dolphin schools. Administrative Rep. LJ-84-31 available from Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038. 56pp.

change noted in response to the ship. In that case, when the vessel was within 800m, the group moved rapidly perpendicular to the path of the vessel and then parallel to and in the opposite direction of the vessel. Observers on the ship saw this porpoise group as they moved rapidly out of the path of the vessel. Observers on the ship also saw 2 of the other 5 groups. Although this sample of behavior is small, movement in response to the survey vessel appeared limited to within 1km of the vessel and, when it occurred, animals did not travel far from their original positions.

Porpoise Density

The probability density distributions of perpendicular sighting distances are shown in Figure 7 for Surveys 1 and 3 and for Beaufort states 0 & 1 and 2. The hazard rate model gave acceptable fits for all sighting distributions ($p > 0.1$) when the truncation criteria was set at 400m (Table 4). For Survey 1, the optimum truncation points were chosen as 400m for sea state 0 & 1 and 800m for sea state 2; for Survey 3, this distance was 400m for both sea state catagories. The fits of these model are also shown in Figure 7. Estimates of density and standard errors are given in Table 4.

Depth Distribution Model

The model of harbor porpoise depth distribution was based on the relative densities of harbor porpoise at different water depths. Ship survey data were pooled into three depth ranges: 18 to 37m (10-20 fathoms), 37 to 55m (20-30 fathoms), and 73 to 110m (40-60 fathoms). Ship surveys are not possible inshore of the 18m isobath, but estimates from aerial surveys[2] show roughly equal density at 0.61 and 1.85km from the shore (the latter corresponding approximately to the 18m isobath). Relative density from ship surveys was measured in the number of sightings per nautical mile of searching effort. Relative densities at 18-37m show no consistent relationship to those at 37-55m (Fig. 8a), but on average these appear to be approximately equal. Relative densities at 18-37m are, however, consistently higher than densities at 73-110m in all 4 areas (Fig. 8b). No harbor porpoise were seen while searching 236km in waters deeper than 110m.

Despite high variability in patterns of depth distribution and lack of ship coverage in shallow waters, some generalizations can be made about the depth distribution of harbor porpoise along the west coast. The relative abundance of harbor porpoise appears to be roughly constant from shore to 55m, to decrease markedly by 73-110m, and to be very low in waters deeper than 110m.

Based on the above relationships, I propose the following preliminary model for the depth distribution of harbor porpoise along the coasts of California, Oregon, and Washington: constant abundance from the coast to the 75m isobath, linearly decreasing abundance from the 75 to 125m isobaths, and zero abundance in waters deeper than 125m (model illustrated in Fig. 8). Because considerable uncertainty exists in this model, I propose two alternative models: 1) constant abundance from shore to 25m, linearly increasing abundance from 25 to 50m, linearly decreasing abundance from 50 to 150m, and zero abundance in waters deeper than 150m; and 2) linearly increasing abundance from the shore to 25m, linearly decreasing abundance from 25m to 125m, and zero abundance in waters deeper than 125m (both illustrated in Fig. 8). Alternative models 1 and 2 are less likely than the primary model given because both conflict with some of the available data. The alternative models do, however, encompass the likely range of relative density values and provide a means to evaluate the sensitivity of the abundance estimate to different models of depth distribution.

To estimate abundance, the depth distribution model must be combined with information about the area within defined bathymetric strata. Therefore, the depth distribution model was re-expressed in terms of relative abundance within the 0-50, 50-100, and 100-300m isobaths. The distribution of depths within each of these intervals was assumed to be uniform, thus for the first depth strata (0-50m), the relative density was estimated as

$$I_1 = \frac{\int_0^{50} i(x)\, dx}{50} \qquad (5),$$

where $i(x)$ = relative density at depth x given by the models in Fig. 8.

The resulting ratios of relative abundance within each interval (I_k in Eq. 4) are given in Table 5.

Fraction of Missed Animals

The experiment on Survey 4 indicates that some trackline groups were seen by one group of observers and were missed by the other. A total of 103 sightings was made by both teams, 33 of which were estimated to be within 100m perpendicular distance from the transect line. Of the 103 total sightings, 85 were detected only by the 5 principal observers, 6 were detected only by the 3 monitor observers, and 12 were detected by both teams. Of the 33 trackline sightings, 20 were detected only by the principal observers, 3 were detected only by the monitor

observers, and 10 were detected by both teams. The Lincoln index estimate of the fraction of trackline porpoise seen by the primary team of 5 observers is thus 0.769 (s.e. = 0.117, 95% C.L. = 0.45 to 0.95). This indicates that roughly 23% of trackline sightings are missed by the principal teams of 5 observers.

Porpoise Abundance

Estimates of porpoise abundance in each of the eight geographic strata are given in Table 6 for the primary model of offshore distribution. Independent estimates are given for Survey 1 and for Survey 3 in each area. Both surveys show similar patterns, with higher abundances in the northern strata (4 to 8) and very low abundance in strata 1 and 3. Despite similar patterns, differences between the paired estimates are, in some cases, large and statistically significant (t-tests, $p < 0.05$). Because Region 8 was not covered on the third survey, it is not possible to compare estimates of total abundance for the entire coast between surveys. The total abundances for Regions 1-7 (Pt. Conception to the Columbia River) are 51,877 (s.e.= 12,382) animals and 34,901 (s.e.= 12,914) animals for Surveys 1 and 3, respectively. The difference between these estimates is not statistically significant (t-test, $p > 0.05$). Pooling the results of the two surveys, the estimate of harbor porpoise abundance between Pt. Conception and Cape Flattery in September of 1984 and 1985 is 49,862 (s.e.= 8,891) animals (Table 6). The same estimate using the alternate models of offshore distribution ranges from 31,456 to 79,425 (Table 7).

DISCUSSION

Distribution

Harbor porpoise are not uniformly distributed between Cape Flattery and Point Conception. Although there are no obvious discontinuities within this range, density varies geographically and temporally. The most dramatic temporal changes are between the two September surveys and the January/February survey (Fig. 1). The coasts of Washington and northern Oregon were found to have relatively high densities of harbor porpoise in September, but, despite excellent sighting conditions, very few porpoise were seen there in January. High densities of porpoise were also seen in Monterey Bay on both September cruises and on Survey 4 in May. This area was intensively surveyed in February, and few porpoise were seen. As can be seen in Figure 1, adjacent areas tended to have similar densities within a survey. Less consistency is found when the same areas are compared between different surveys.

The apparent changes in distribution could be caused by small changes in depth distributions. The majority of survey

effort was along the 18m isobath. A large fraction of animals could be missed if their depth distribution changed by 10m or less. More information on depth distributions is needed before the apparent temporal changes in geographic distribution can be interpreted.

Porpoise Density

Estimates of harbor porpoise density ranged from 0.03 to 2.6 animals/km^2 along transect lines in the eight geographic regions (Table 4). In another study, Taylor and Dawson (1984) found 1.2 to 5.9 porpoise/km^2 at study sites in Glacier Bay, Alaska. Flaherty and Stark (1982) estimated 0.8 to 1.6 porpoise/km^2 in Washington Sound. Gaskin, Read, Watts, and Smith (1985) calculate values ranging from 0.0 to 13.3 porpoise/km^2 along transect lines in the Bay of Fundy and Gulf of Maine. Densities in the present study are therefore within the range of densities found in other areas.

Of the areas surveyed, porpoise density is highest in northern California and Oregon. The highest density was seen in northern Oregon (Region 7) during Survey 1. The second highest density was observed in northern California between Bodega Head and Cape Mendocino (Region 4) on Survey 3.

Two areas in central California (Region 1 and 3) were found to have very low densities. Region 1 includes the Big Sur coastline from Pt. Conception to Pt. Sur. This area is characterized by steep depth gradients and hence has little habitat that is suitable for harbor porpoise. In Region 1, 378km of trackline were surveyed at Beaufort states 0-2. Region 3 includes the Gulf of the Farallons with its broad coastal shelf within the 100m isobath. However, only 175km were surveyed there. Region 3 thus includes a large area of suitable habitat, only a small portion of which was actually surveyed. Therefore, although Regions 1 and 3 were both identified as low density areas, more confidence can be placed on this conclusion for Region 1 than for Region 3.

Abundance

The size and behavioral characteristics of harbor porpoise make estimating their abundance difficult. Harbor porpoise are small, occur in groups of only a few individuals, surface without conspicuous splashes, and their distribution is extremely patchy. Even with 5 observers, the effective path width that can be searched from a ship is less than 1 km, and that path width decreases very rapidly in rougher sea states. All of these factors contribute to high variability in the abundance estimates presented here. Seasonal and year-to-year changes in the distribution of harbor porpoise may also contribute to the variability seen within geographic strata. These are, however,

the best (and, for some regions, the only) estimates of harbor porpoise abundance for the west coast.

Although there are no prior estimates for Oregon or Washington coasts, Dohl et al. (1983) have estimated harbor porpoise abundance in central and northern California. Their estimates range from 3,000 porpoise in autumn to 1,600 in summer, which correspond (approximately) to the pooled estimate of 11,457 for Regions 1 to 4 based on the present study. There are, however, several problems with the application of their methods to the estimation of harbor porpoise abundance. In a direct comparison with shore counts, Kraus et al. (1983) showed that observers on aircraft saw only 10-20% of porpoise groups. Dohl et al. (1983) did not apply a correction to account for porpoise groups that are submerged at the time the aircraft passed. Also, Dohl et al. (1983) did not stratify estimates by distance from shore or depth. Although most of their harbor porpoise sightings were within 0.5km (0.25 NM.) of shore, their density estimates were extrapolated to an area extending 166km from the coast. Estimates from the current study are based on better methodology than previous estimates.

In addition to exposed coastal habitats, harbor porpoise are also found in bays along the coasts of California, Oregon and Washington. Goetz (1983) reported that porpoise are found throughout the year in Humbolt Bay, CA. Harbor porpoise have been seen in San Francisco Bay, but are described as rarely present[5]. Abundance of harbor porpoise in inland waters may, however, vary seasonally (Taylor and Dawson 1984). No estimates exist for the total number of porpoise inhabiting bays. Survey effort in the present study was limited to exposed coastal areas (including Monterey Bay, but excluding San Francisco Bay, Humbolt Bay, Coos Bay, Yaquina Bay, the mouth of the Columbia River, Willapa Bay, and Grays Harbor). If harbor porpoise density in bays were the same as that which was observed along the 18m isobath, population sizes presented here could be increased by approximately 3.1% to account for porpoise inhabiting 900 km^{-2} (the approximate combined area of Humbolt Bay, Coos Bay, Yaquina Bay, the mouth of the Columbia River, Willapa Bay, and Grays Harbor).

Line Transect Assumptions

Biases in abundance estimates can be an even greater problem than high variability. In the case of estimates

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[5] Szczepaniak, I. D. and M. A. Webber. 1985. Status of the harbor porpoise (Phocoena phocoena) in the eastern North Pacific, with an emphasis on California. Contract report to the Center for Environmental Education, Washington, D.C. 52pp.

presented here, biases could be introduced if the assumptions of line transect sampling are not met (Burnham et al. 1980; Hammond and Laake 1983). Of these assumptions, the most relevant to this study are: 1) the area must be sampled randomly or the animals must be randomly distributed within the area; 2) all groups on the track-line must be detected; and 3) group size must be estimated without error. These assumptions will be addressed below.

To address the first assumption (random distribution), cruise tracks were chosen to systematically cover the coast from Pt. Conception to Cape Flattery. Because the surveys were designed to cover the entire longshore range of harbor porpoise in this area, randomly placed survey tracks were deemed unnecessary. Although some areas of the coast were missed, these locations were determined by weather and were presumably not correlated with porpoise abundance. Surveys were, however, limited to a very narrow strip along the 18m isobath. Initially, the choice of this survey track was based on the observation that, in aerial surveys, porpoise were usually found within 0.5km (0.25 NM.) of the shoreline in California (Dohl et al. 1983). The 18m isobath was simply the shallowest reasonable working depth for the NOAA survey ships. In the course of these surveys, it was found that porpoise are commonly distributed much further from the coast than 0.5km and that one survey track could not adequately cover their habitat. The offshore distribution of harbor porpoise is not random, but is related to water depth, distance from shore, or both. The model from which I extrapolated density at 18m to density at other depths was based on a rather limited sample at a few locations along the coast. The assumption of random search in offshore areas was not met. Evaluating the effect of this requires additional work.

The second assumption is that 100% of the animals in the immediate vicinity of the trackline were detected. Animals near the trackline can be missed because they move away from the path of the ship, because they do not surface within the visual range of the observers, or because the observers fail to detect animals that do surface. Any of these would result in a negative bias and an underestimation of porpoise abundance using line transect methods. These three problems are considered in more detail.

West-coast harbor porpoise are commonly said to avoid vessels (Flaherty and Stark 1982, Szczepaniak and Webber[7]) and may be missed or not counted in the proper perpendicular distance category for this reason. On the surveys, the majority of porpoise were oriented roughly parallel to the ship at the time they were sighted and were swimming parallel to the ship and in the opposite direction.[2] This was also observed in one instance from the helicopter; however, in that case the group first moved perpendicular to the path of the ship. These observations indicate that harbor porpoise are reacting to the ship before

they are seen by observers. Reaction to and avoidance of the ship does not necessarily mean that estimates of trackline density are biased if animals are detected before they travel an appreciable distance from the trackline. In several instances, porpoise surfaced within 50m of the ship and directly in its path. These animals appeared startled and quickly moved to avoid the ship. In these cases, the rapid movement of the animals and splashes associated with that movement made the animals more visible to observers. Because avoidance behavior may make porpoise more visible and because the distributions of perpendicular distance show only a single mode (at the origin), vessel avoidance probably does not introduce a large bias in harbor porpoise abundance estimation. More work is needed in this area.

Porpoise near the trackline may also be missed if they either inadvertently or intentionally do not surface within the visual range of the observers. Typical mean dive times for harbor porpoise have been measured as 1.5-2.3 minutes (Glacier Bay, Alaska; Taylor and Dawson 1984), 1.8 minutes (northern Oregon; B. Taylor, pers. comm.), and 0.4-1.4 minutes (Bay of Fundy, Watson and Gaskin 1983). The ships' speed during surveys was approximately 18.5 km/hr. or 310 m/min; thus, in 2 minutes the ship would travel 620m. The average distance at which animals were first seen was 704m from the ship. If individual dive times were appreciably longer than 2 minutes, some trackline individuals would not be detected by observers. In data collected in northern Oregon, 16% of dive times were greater than 2.5 minutes (B. Taylor, pers. comm.). In addition, harbor porpoise have been known to increase dive times up to 7 minutes in the presence of boat traffic (Flaherty and Stark 1982). Helicopter observations in Monterey Bay indicated that porpoise groups did not extend dive times in the presence of the survey vessel[2]. This area might not be representative, however, because porpoise may be more accustomed to vessel traffic there than along the majority of the coast. It is likely that some porpoise are missed because they do not surface near the vessel; however, it is not possible to quantify this source of bias without additional study.

Trackline animals may be missed even if they do not avoid the ship and do surface within visual range of the observers if their surfacing is not detected. In another study comparing ship surveys to aerial and shore surveys, Kraus et al. (1983) found that observers on ships saw only about 50% of the porpoise in an area. In that study, however, ship observers stood only 2.5m above the sea surface (versus 10m in this study), and the estimate of 50% was based on all groups, not just on trackline animals. Based on the experiment using monitor observers in the present study, an estimated 23% of porpoise that surface within 100m of the trackline are missed by the usual team of 5 observers.

The third critical assumption is that group size is estimated without error. In the case of harbor porpoise, group size is small and estimates are typically based on actual counts. For tropical dolphins, which school in groups of several hundreds, the problem of group size estimation is more acute (Holt and Powers 1982, Hammond and Laake 1983, Holt[3]). Only in two instances did porpoise group size exceed 20: in Monterey Bay and near Pt. Arena, both in California. Excluding these two sightings, mean group sizes are 2.05, 2.33, 2.03, and 1.59 for Surveys 1, 2, 3, and 4 (respectively); including the two sightings, means are 2.30 and 2.26 for Surveys 1 and 3. These values are comparable to other estimates of mean group size for coastal populations of harbor porpoise: 2.2 based on aerial surveys in California (Dohl et al. 1983), 2.6 based on ship surveys in the Gulf of the Farallons (Szczepaniak and Webber, pers. comm.), 2.3 based on shore surveys in northern Oregon[2], and 2.75-3.23 based on aerial surveys along California, Oregon, and Washington[2]. The consistency of all these estimates from different platforms indicates that group size estimation from ships is not likely to be a major source of bias in abundance estimation.

Variance Estimation

Although the estimates of standard error for abundance and density are very high, these may still be underestimates because several possible sampling errors were not considered. The model upon which relative abundance in the various depth strata was based is too crude to allow reasonable estimates of its variability. Estimates based on alternate models of depth distribution indicate that abundance estimation is relatively sensitive to the choice of models. Additional field work may help refine this model and allow estimation of variance for the parameters I_k in Equation 4. Variance was also not estimated for the percentage of missed animals. Additional field work is needed to refine this estimate, and new analytical methods are needed to calculate its variance.

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Table 1. Dates, beginning and ending ports, and northern and southern extremes of porpoise survey efforts.

	Dates	Ports	Northern/Southern Extremes
Survey 1	Sept. 4, to Sept. 15, 1984	San Diego San Diego	Cape Flattery, WA Point Conception, CA
Survey 2	Jan. 24, to Feb. 9, 1985	Seattle San Diego	Cape Flattery, WA Point Conception, CA
Survey 3	Sept. 3, to Sept. 17, 1985	San Diego San Diego	Columbia River, OR Point Conception, CA
Survey 4	Apr. 24, to May 5, 1986	San Francisco San Diego	Pt. Arena, CA Point Conception, CA

Table 2. Areas (km^2) for the regions located between the 0, 50, 100, and 300m isobaths and for kelp beds from Point Conception, California to Cape Flattery, Washington. Geographic regions refer to those presented in Figure 5. The 0-50m stratum includes kelp bed areas, but does not include most bays (see Discussion).

Geographic Region	Kelp Bed Area	Area 0-50m	Area 50-100m	Area 100-300m
1	36	1696	1130	1404
2	7	1219	1380	1325
3	9	1950	1672	1428
4	16	1614	1047	2984
5	0	2822	1871	2476
6	4	1435	2424	5085
7	3	1707	1882	4968
8	48	4656	2850	6551

Table 3. Estimated values of the probability density functions evaluated at zero perpendicular distance, f(0). Estimates are based on the hazard rate model and were made for truncation distances of 400, 800, 1600, and 3200m. Estimates are given only if the model gave an acceptable fit to the data ($p > 0.1$). Asterisks indicate f(0) values with the lowest coefficient of variation (parentheses).

Survey	Sea State	Truncation Distance 400m	800m	1600m	3200m
1	0 & 1	7.85 *	5.31	4.31	-
		(0.23)	(0.29)	(0.24)	-
1	2	10.48	8.15 *	7.09	5.78
		(0.59)	(0.21)	(0.33)	(0.51)
2	0 & 1	4.51 *	3.10	2.69	-
		(0.22)	(0.66)	(0.31)	-
3	2	6.97 *	-	-	-
		(0.19)	-	-	-

Table 4. Density estimates, D, for harbor porpoise (km^{-2}) along the 18m isobath in each of eight geographic strata. Density was calculated per Equation 2 using estimates of f(0) (Table 3) which had the lowest coefficients of variation. Standard errors are in parentheses.

Geographic Region	Survey 1		Survey 2		
	Beaufort 0 & 1	Beaufort 2	Beaufort 0 & 1	Beaufort 2	Pooled Estimates
1	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.04 (0.02)
2	1.1 (1.0)	0.0 (0.0)	0.6 (0.5)	0.1 (0.1)	0.51 (0.30)
3	-	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	0.03 (0.03)
4	-	2.5 (1.0)	0.0 (0.1)	6.7 (7.2)	2.83 (1.69)
5	-	2.1 (1.3)	0.8 (0.6)	0.6 (0.3)	0.91 (0.32)
6	1.4 (0.8)	2.0 (0.6)	2.5 (0.8)	2.6 (0.9)	2.22 (0.40)
7	7.9 (3.4)	0.8 (0.6)	2.5 (0.6)	1.3 (0.7)	2.64 (0.78)
8	1.8 (0.8)	0.0 (0.0)	-	-	1.09 (0.45)
Total	2.5 (1.1)	1.3 (0.6)	0.8 (0.4)	1.2 (0.5)	1.33 (0.30)

Table 5. Relative porpoise densities, I_k, in the three depth strata that were used to calculate abundance. Densities are relative to that estimated for the 18-fathom transect line (relative value of 1.0).

Distribution Model	Depth Strata 0-50m I_1	50-100m I_2	100-300m I_3
Primary model	1.000	0.875	0.031
Alternative model 1	1.250	1.500	0.167
Alternative model 2	0.687	0.500	0.016

Table 6. Estimated abundance of harbor porpoise in each of the eight geographic strata based on the primary model of offshore distribution. Estimates for Beaufort 0 & 1 and for Beaufort 2 were computed separately and then averaged, weighting by transect length. Pooled estimates for the eight strata were obtained as a average of the two surveys, weighting by transect length. All estimates are adjusted for missed animals. Standard errors are in parentheses.

Geographic Region	Survey 1	Survey 3	Pooled Estimates
1	0	160 (87)	123 (66)
2	2660 (2417)	1032 (716)	1616 (981)
3	0	157 (163)	115 (119)
4	8388 (3599)	11045 (11969)	9603 (5811)
5	12568 (7767)	3684 (1579)	5371 (1953)
6	8729 (2634)	12317 (3555)	10699 (2285)
7	19532 (8201)	6506 (2801)	12013 (3826)
8	10321 (4543)	- -	10321 (4543)
Totals			
Regions 1-3	2660 (2417)	1350 (739)	1854 (991)
Regions 1-7	51877 (12382)	34901 (12914)	39541 (7643)
Regions 1-8	62198 (13189)	- -	49862 (8891)

Table 7. Estimated abundance of harbor porpoise in central California (Regions 1-3) and along the entire coast (Regions 1-8) based on two alternate models of offshore distribution. All estimates are adjusted for missed animals. Standard errors are in parentheses.

	Survey 1	Survey 3	Pooled Estimates
Alternate Model 1			
Regions 1-3	4113	2070	2855
	(3737)	(1141)	(1531)
Regions 1-8	98559	-	79425
	(20722)	-	(13980)
Alternate Model 2			
Regions 1-3	1669	850	1166
	(1516)	(464)	(622)
Regions 1-8	39293	-	31456
	(8358)	-	(5655)

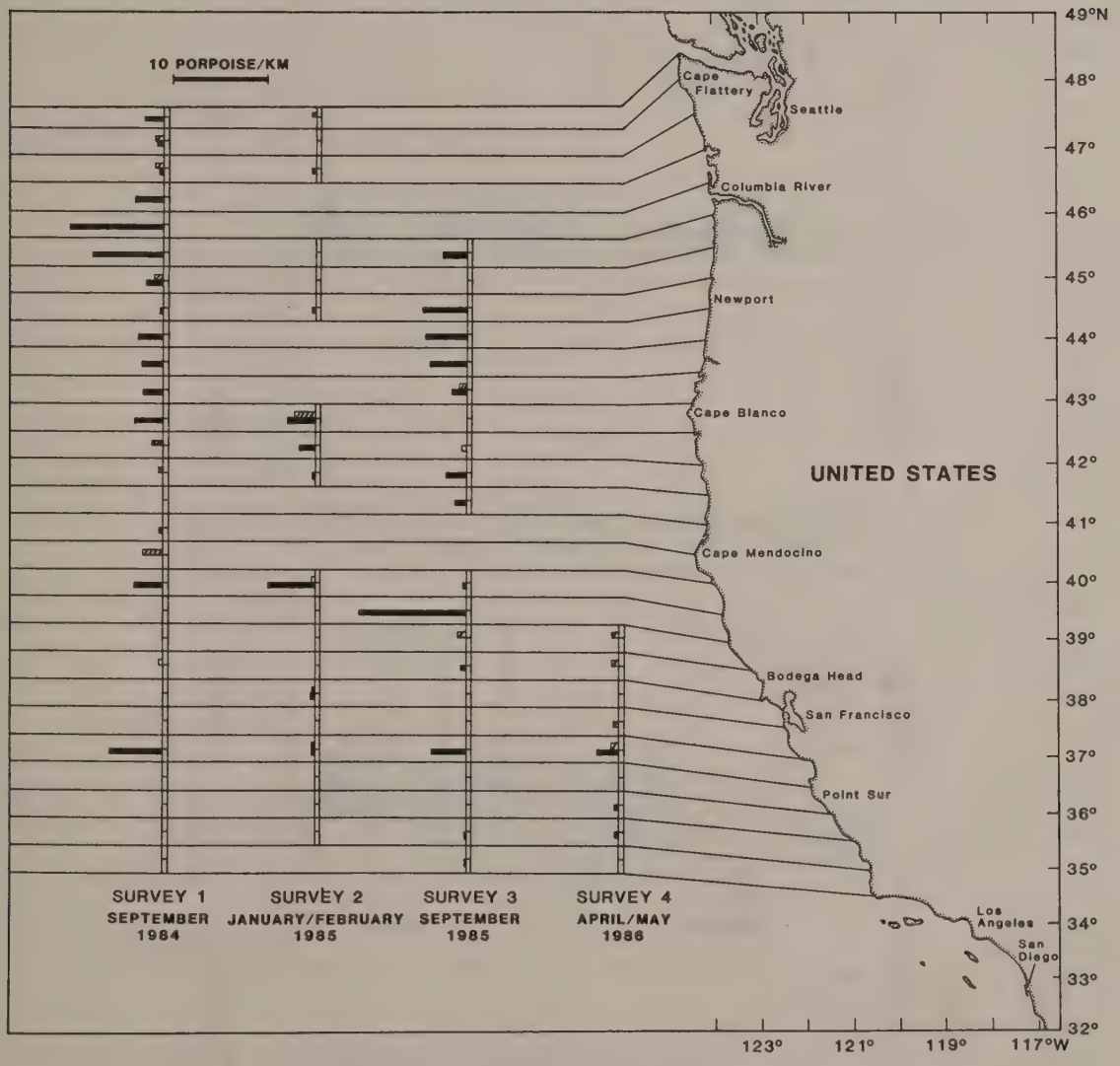

Figure 1. Relative sightings per kilometer based on 30-minute latitudinal strata. Lines parallel to the coast indicate areas that were surveyed. Histograms indicate relative numbers of porpoise seen per kilometer of transect, with solid lines indicating relative numbers in calm seas (Beaufort 0, 1 and 2) and hatched lines indicating relative number in rough seas (Beaufort 3, 4, and 5).

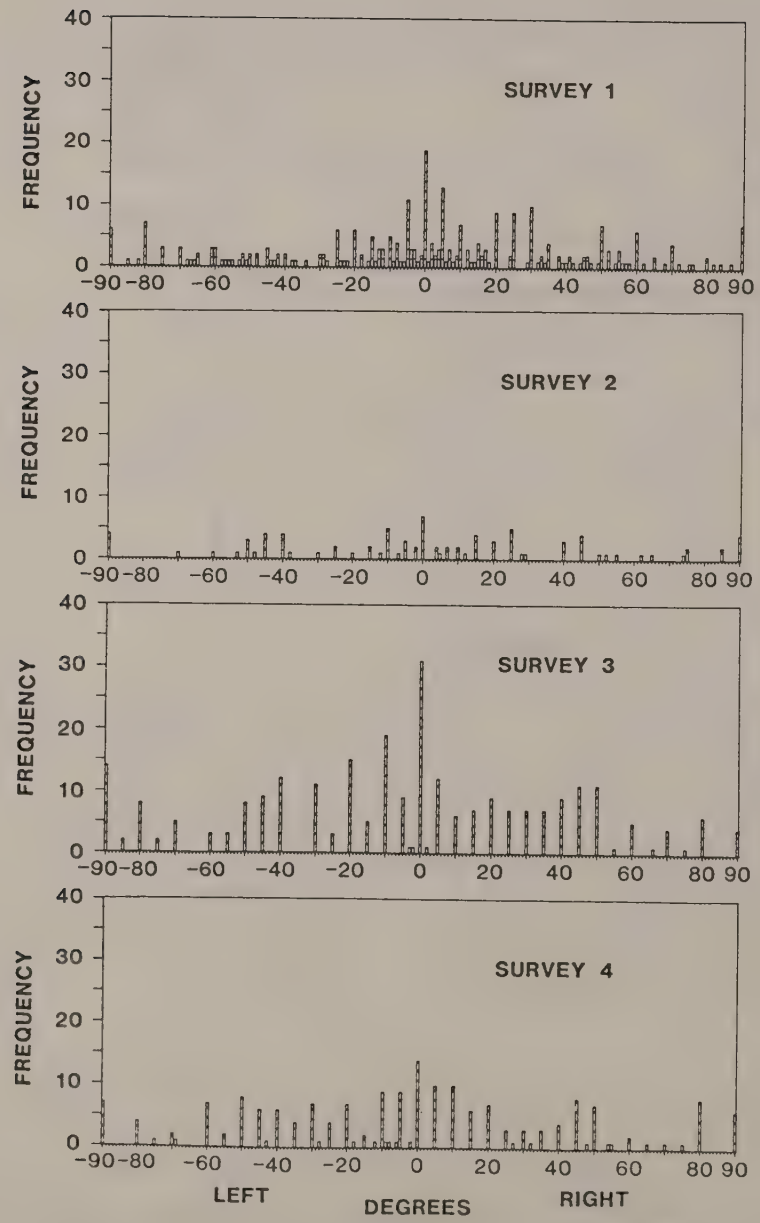

Figure 2. Frequency distribution of radial angle estimates for groups of harbor porpoise at the time of first sightings. Angles are relative to the bow of the ship (zero degrees).

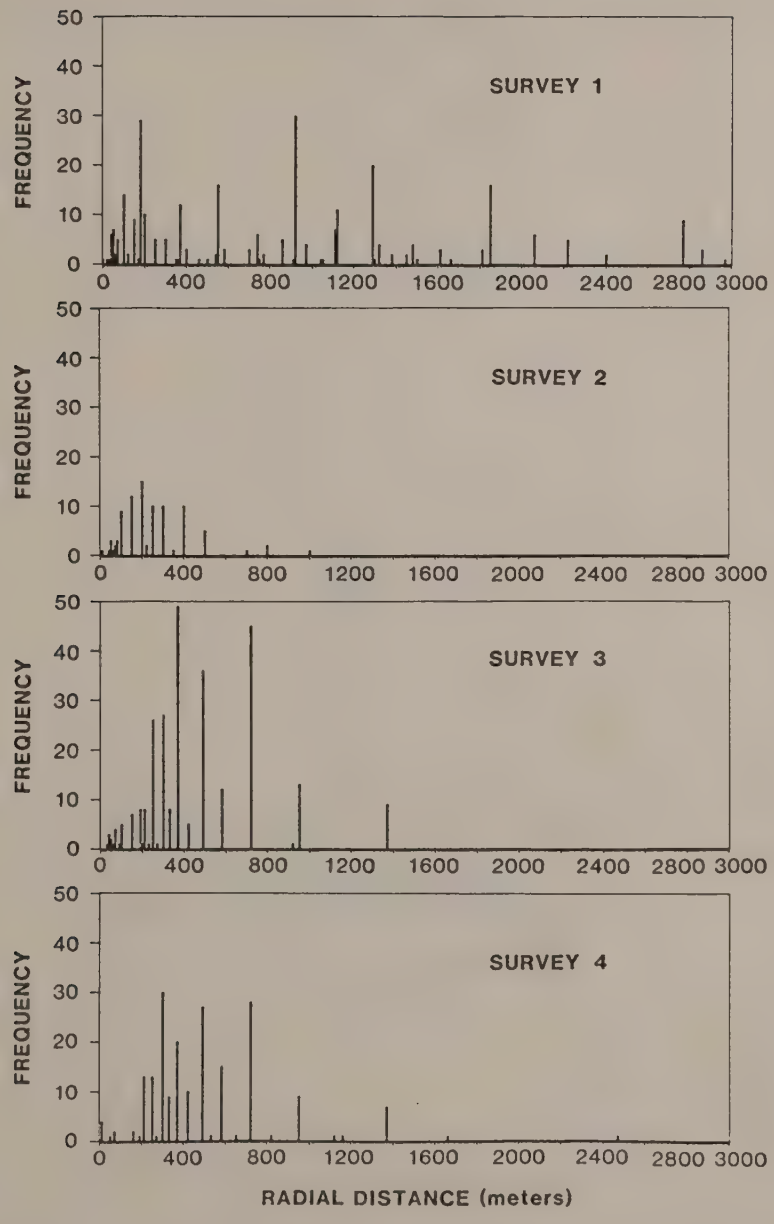

Figure 3. Frequency distribution of radial distance estimates from the ship to groups of harbor porpoise at the time of first sightings.

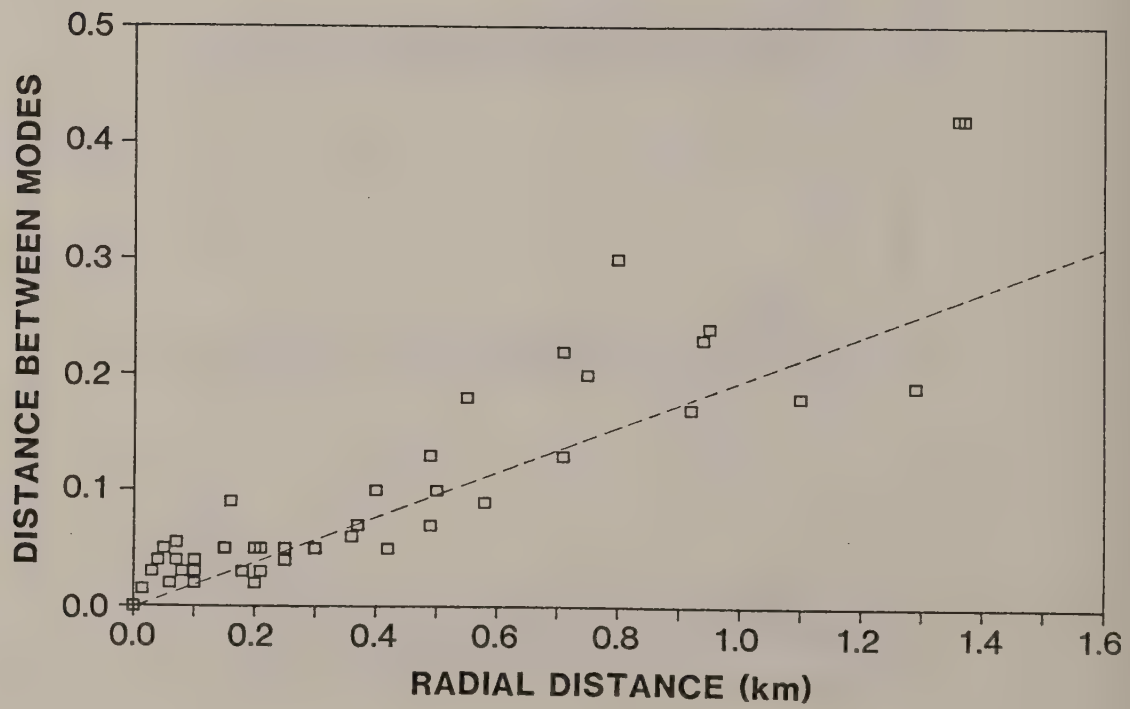

Figure 4. Distance between modes in estimates of radial distance (from Fig. 3) expressed as a function of radial distance. Broken line indicates the model of rounding error that was used in estimating smeared perpendicular distances (error is equal to 0.2 times estimate).

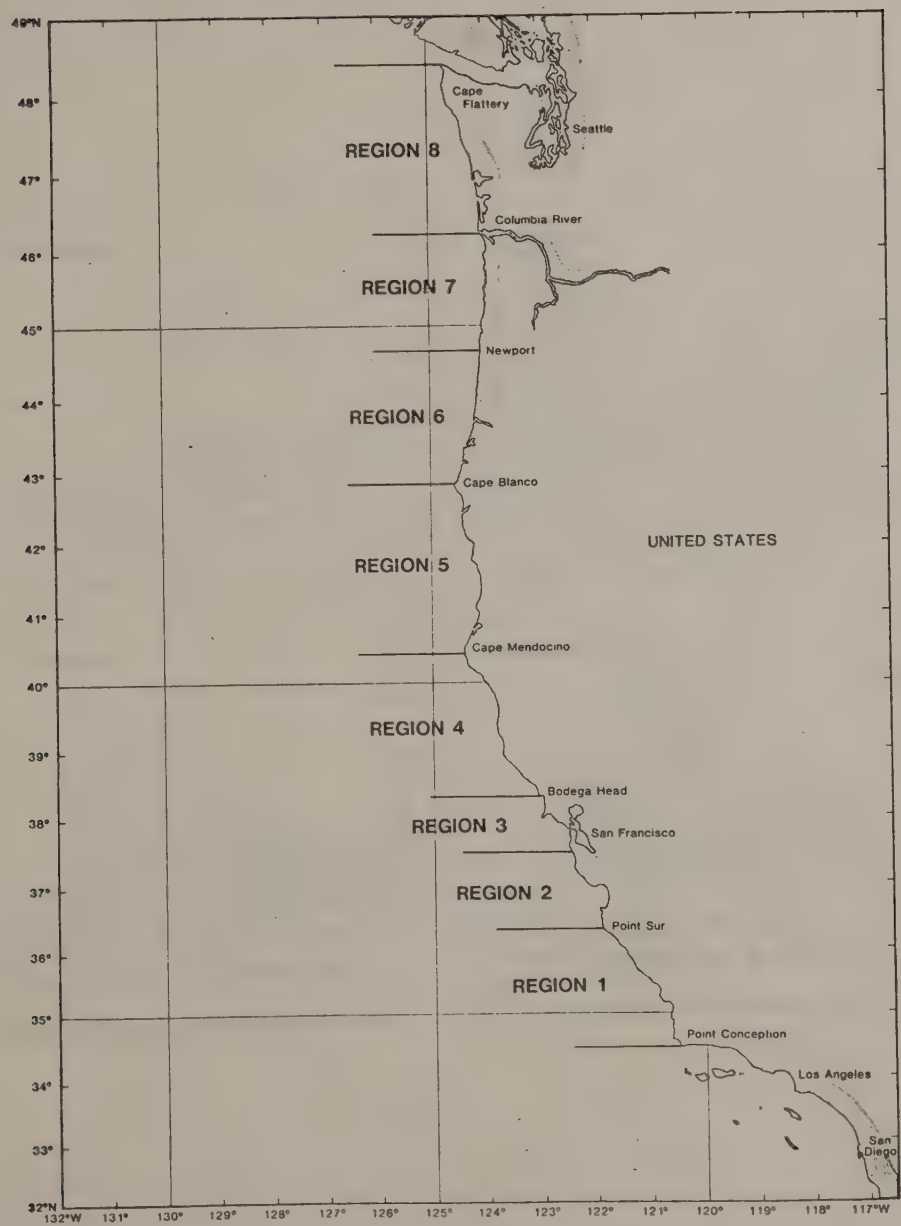

Figure 5. Geographic regions used as strata in abundance estimation.

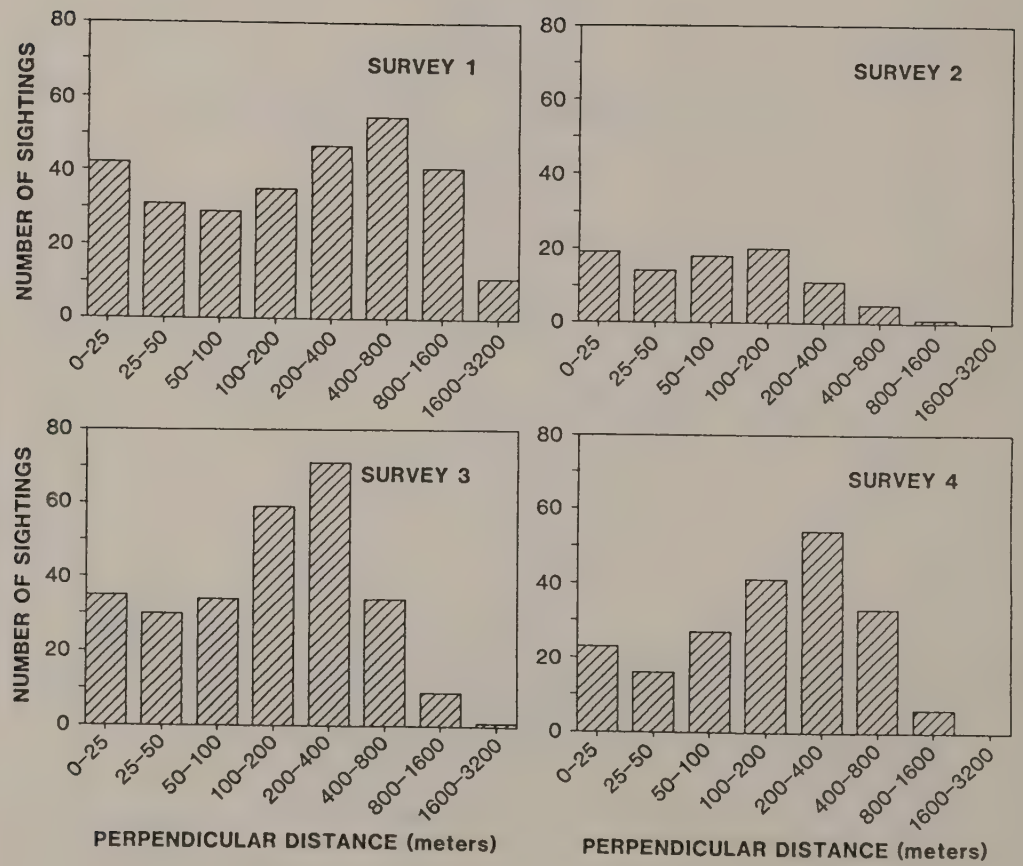

Figure 6. Frequency distributions of harbor porpoise group sightings as a function of perpendicular sighting distance.

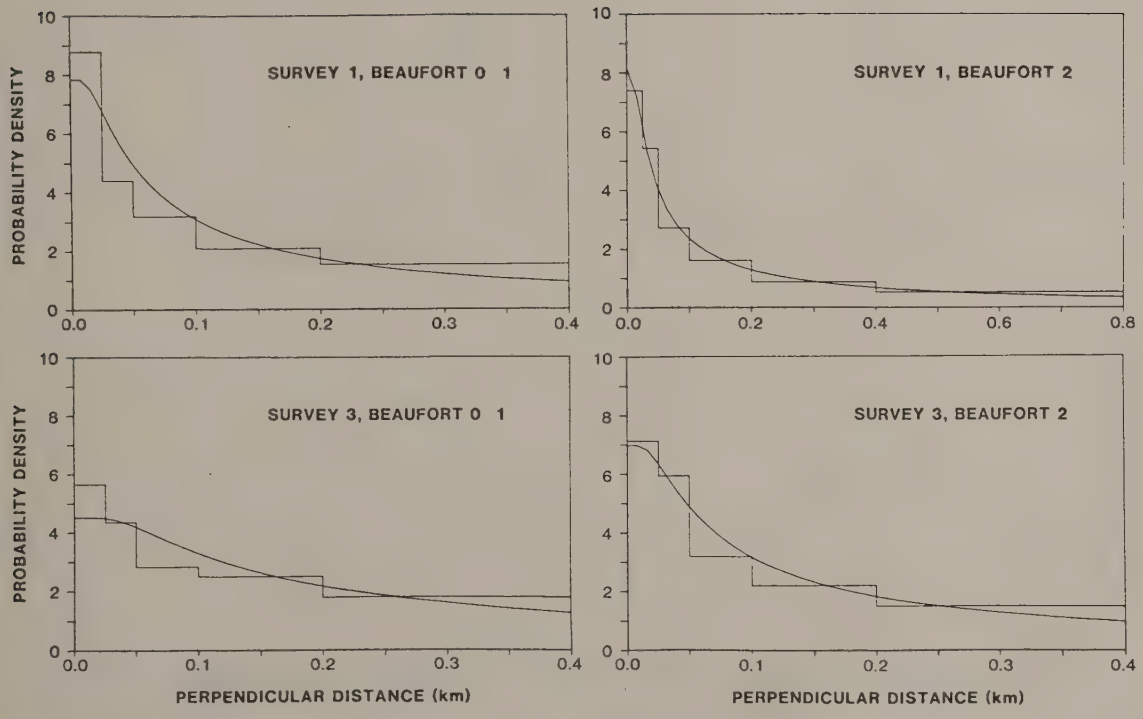

Figure 7. Probability density distributions for perpendicular sighting distances. Histograms indicate observed distributions and solid lines indicate the best fit of the hazard rate model to these data.

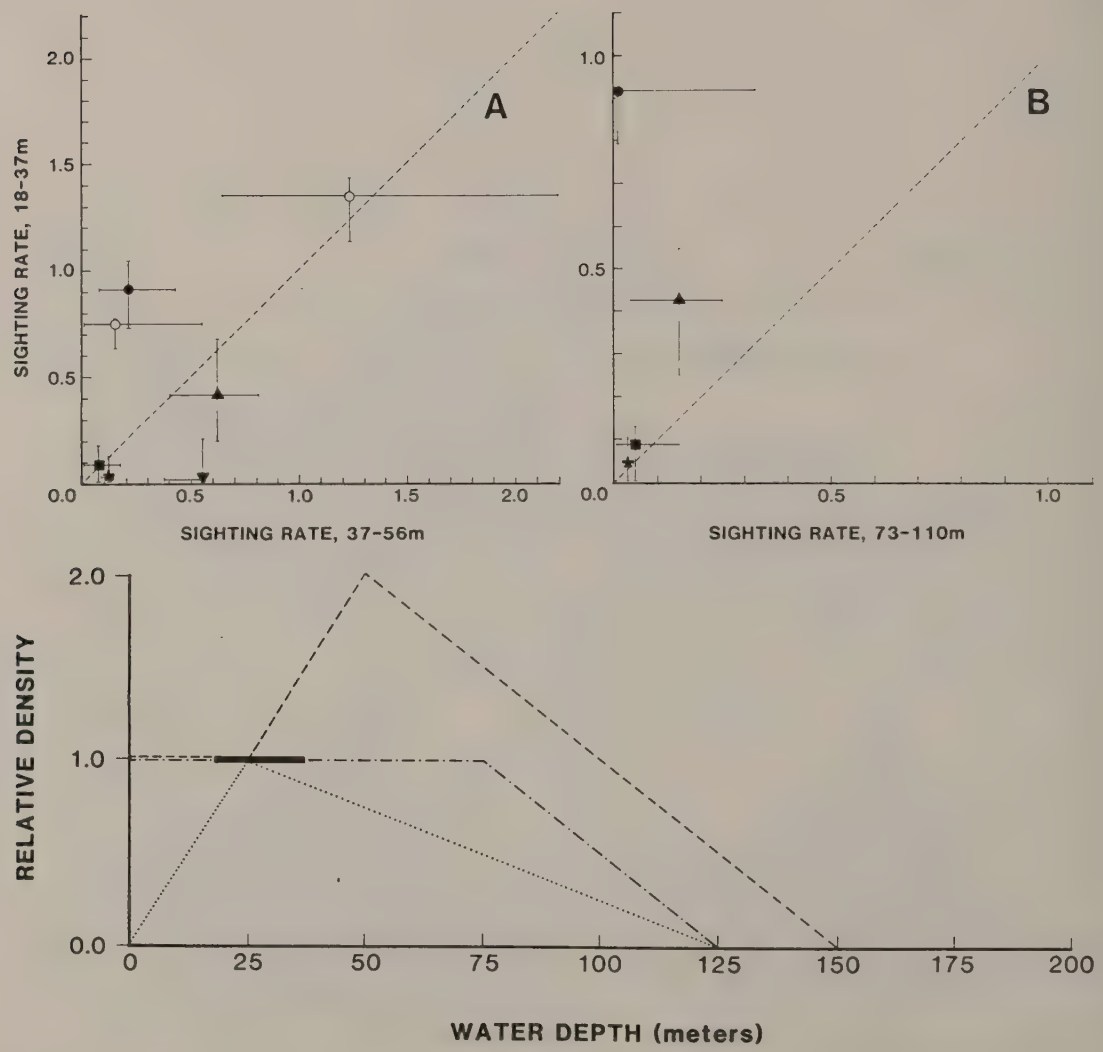

Figure 8. Proposed models for the depth distribution of harbor porpoise. Density at 18-37m is assumed to be known and is given a relative value of 1.0. Included are the primary model (-·-·-), and two alternate models (----- and ·····) of depth distribution (see text). Models were based on observed sighting rates (sightings per N.M.) at 37-56m and 73-110m relative to sighting rates at 18-37m in the same location (panels A and B, above). Locations include Pt. Reyes (* , LaBarr and Ainley 1975), Fort Bragg, CA (■), Coquille Pt., OR (▲), Tillamook Head, OR (●), Russian River, CA (▼), and Monterey Bay, CA (o). Confidence limits on sighting rates were based on 95% probability contours for binomial sampling of n_1 sightings (at one depth) out of a possible sample of $n_1 + n_2$ (the number of sightings at both depths) (Conover 1971, Table 4).